THE RÔLE OF ISOLATION IN THE FORMATION OF A NARROWLY LOCALIZED RACE OF DEER-MICE (PEROMYSCUS).*

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No one who has critically examined large numbers of specimens, belonging to such a widely distributed and diversified genus as *Peromyscus,* can fail to be impressed with two facts. First, the differences upon which the so-called "subspecies" are based are real and obvious ones. But, secondly, the actual subspecies which are recognized and named are necessarily highly artificial groups. On the one hand, each subspecies intergrades with others to such an extent that the assignment of a given specimen to one or the other group is often quite arbitrary. And on the other hand, even these "subspecies" themselves are far from being elementary. They are composite groups, comprising, in many cases, a number—perhaps a great number—of distinguishable local types. The word *distinguishable* is here used in a qualified sense. It is likely that the distinctions would commonly be obvious just in proportion as the collections were made at points which were remote from one another.

Indeed, it has been said by one who has monographed this genus of mice[1] that "classification becomes . . . like dividing the spectrum and depends largely upon the standards set, for, theoretically at least, the possibilities of subdivision are unlimited (p. 17)."

None the less, it is generally believed that where well-marked physical or other barriers are interposed between two groups of individuals, this continuous intergradation

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[1] Osgood, "Revision of the Mice of the American Genus, *Peromyscus,*" North American Fauna, No. 28. Washington, 1909.

of racial characters may be largely interrupted. It is the object of this paper to discuss a case of this sort which I have had the opportunity of studying during the past year.

The subspecies *Peromyscus maniculatus rubidus,* according to Osgood,[2] who first described it, occupies a strip of varying width on the "coast of California and Oregon from San Francisco Bay to the mouth of the Columbia River." In discussing certain local variations shown by this subspecies throughout its range, the same writer states that "six specimens from the Outer Peninsula, near Samoa, Humboldt Bay, are decidedly paler than others from the neighboring redwoods. They evidently represent an incipient and very local subspecies, and well illustrate the plasticity of the group to which they belong." Osgood further remarks that "a careful study of this variation and the local conditions doubtless would prove instructive" (p. 66).

During the latter part of May, 1916, I trapped on two consecutive nights in the neighborhood from which Osgood obtained his six "aberrant" specimens of *rudibus.*[3] About one hundred live-traps were set on each occasion. Twenty-eight specimens were taken, of which twenty-one were later available for skinning and for careful measurement. These last were all in either mature or adolescent pelage, and were about evenly divided in respect to sex.

The distinctness of this race from the *rubidus* of the redwood forests on the mainland was evident from a casual inspection of the living mice. A more careful comparison of freshly killed specimens from the two localities, and later of their prepared skins, justifies the following generalizations. These impressions were formed independently by several other persons to whom I showed the specimens, and were confirmed by more careful ex-

[2] *Loc. cit.,* p. 65.

[3] The trapping was done between one and two miles northwest of the village of Samoa. Besides these *Peromyscus,* the only other animal caught was a single specimen of *Microtus.*

amination and measurement. (1) The Samoa lot, as a whole, were paler than the redwood lot; (2) the tails of the former were shorter, and (3) the ears were longer.

To consider first the coat color, the mean difference between the two series of skins is evident at a glance. Likewise, it is plain that the palest Samoa specimen is paler than the palest Eureka (redwood) specimen, and that the darkest among the former is paler than the darkest among the latter. It must be admitted, however, that the two series overlap rather broadly,[4] the darker skins of the Samoa stock being as dark as or darker than the paler ones of the Eureka stock.

An attempt to express the color of a mammal's pelage in terms of any set of "standard" colors is beset with great difficulties. Instead of a uniformly tinted, plane surface, we have to do with a mixture of variously colored hairs, further diversified by minute shadows and reflections. I have, nevertheless, endeavored, in a rough way, to "match" the colors of these two races with those of Ridgeway's "Color Standards and Color Nomenclature."[5] In the Samoa race, the general tone of the lateral regions of the body lies between the "tawny olive" and "Saccardo's umber," that of the dorsal darker stripe being not far from "sepia." In the Eureka mice, the lateral regions range from "Saccardo's umber" to "sepia," the dorsal stripe being of a depth somewhere between "sepia" and black. These comparisons will at least enable the reader to judge of the degree of difference between the two racs.[6]

As regards the tail, it was plain without measurement that the average length of this member was greater in the

[4] I have at present for reference twenty-one skins of the Samoa lot and thirty skins of wild adults from the redwoods. Ten of the latter individuals were trapped and skinned at about the same time as the former, so that the factor of season may be disregarded.

[5] Washington, 1912. Published by the author.

[6] In my further studies of *Peromyscus* I plan to employ two revolving color-wheels, on one of which the skin itself will be rotated, on the other sectors of black, white and various primary colors. This apparatus is now being tested by Mr. H. H. Collins and myself.

Eureka than in the Samoa race, though here again the difference related to averages and did not hold for all individual cases.

A comparison of the mean figures for *absolute* tail length in two series of mice is not entirely justifiable, particularly if the two lots of individuals differ somewhat in mean body size. But the *relative* tail lengths (expressed as percentages of body-length) may be fairly compared, since there is good evidence that these ratios remain nearly constant after the first few months of life. The following table allows of a comparison between the two races, in respect to this character:

	Number of Cases	Mean (Percentage)	Standard Deviation
Eureka (males)	83	104.39 ± 0.37	4.95
Eureka (females)	53	103.60 ± 0.54	5.85
Samoa (sexes combined)	21	97.48 ± 0.94	6.38

The differences between the Samoa lot (sexes combined) and the Eureka males and females are 6.91 per cent. and 6.12 per cent., respectively. These differences are about seven and six times their probable errors, respectively. Their significance may therefore be regarded as fairly certain, despite the small numbers comprised in the Samoa series.

As regards foot-length, the two races do not differ significantly. But the ear, as already stated, is appreciably longer in the Samoa mice, this difference being perceptible, even without measurement. Here, as in the case of tail-length, a simple comparison of gross averages for the two groups would be unjustifiable. But in the present instance, the conversion of the absolute values into percentages of body-length would be equally unjustifiable, since the growth of the ear is not at all proportionate to that of the body as a whole. We must therefore resort to the method of "size groups," *i. e.*, we must divide each of our two lots of animals into small groups comprising individuals of nearly equal size.

In the case at hand, we have fifteen groups, or rather

pairs of groups, within which a comparison of average ear-length is possible. In twelve cases the mean figure is greater for the Samoa mice, in two cases it is greater for the Eureka mice, while in one case the two figures do not differ appreciably. The probabilities against such a preponderance being due to chance are of course high. The mean difference in ear-length between the two lots, computed according to a method described by me in an earlier paper,[7] is 0.87 mm. Those who have made careful measurements of mice will regard such a difference in the length of this appendage as far from trivial.

Let me now say something as to the environmental conditions under which these two races of *rubidus* live. Those which I have designated as the "Eureka" or "redwood" race were trapped by me during two different years, within a distance of two miles from the southern limits of the city of Eureka, California. The region is one covered in large part by redwood forest, most of which is of second growth, although there are some small areas that have never been logged. The predominant tree is the redwood (*Sequoia sempervirens*), but several other conifers are common, the most abundant of these being the Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga taxifolia*), and lowland fir (*Abies grandis*). The red alder (*Alnus rubra*), cascara (*Rhamnus purshiana*), waxberry (*Myrica californica*), red elderberry (*Sambucus racemosa*), and a willow (*Salix hookeriana*) appear to be the chief non-coniferous trees of this district.[8] The "wild lilac" (*Ceanothus thyrsiflorus*) is likewise common in some of the more open areas, often reaching the proportions of a small tree.

Except in recently cleared tracts, the region is one of dense underbrush, the shrubbery and vines forming, in fact, a veritable jungle which is frequently hard to pene-

[7] *Journal of Experimental Zoology*, Vol. 18, April, 1915, particularly, pp. 341 et seq.

[8] For the determination of many of the plants referred to in this paper I am indebted to Professor H. M. Hall, of the University of California, and to Mr. J. P. Tracy, of Eureka.

trate. Here we meet with the thimble-berry (*Rubus parviflorus* var. *velutinus*), the salmon-berry (*Rubus spectabilis* var. *menziesii*), huckleberry (*Vaccinium ovatum*), red bilberry (*V. parvifolium*), salal (*Gaultheria shallon*), and in the more open areas the blackberry (*Rubus vitifolia*). Two ferns (*Aspidium munitum* and *Pteris aquilina*) are extremely abundant, the latter in particular forming dense growths higher than a man's head. In the

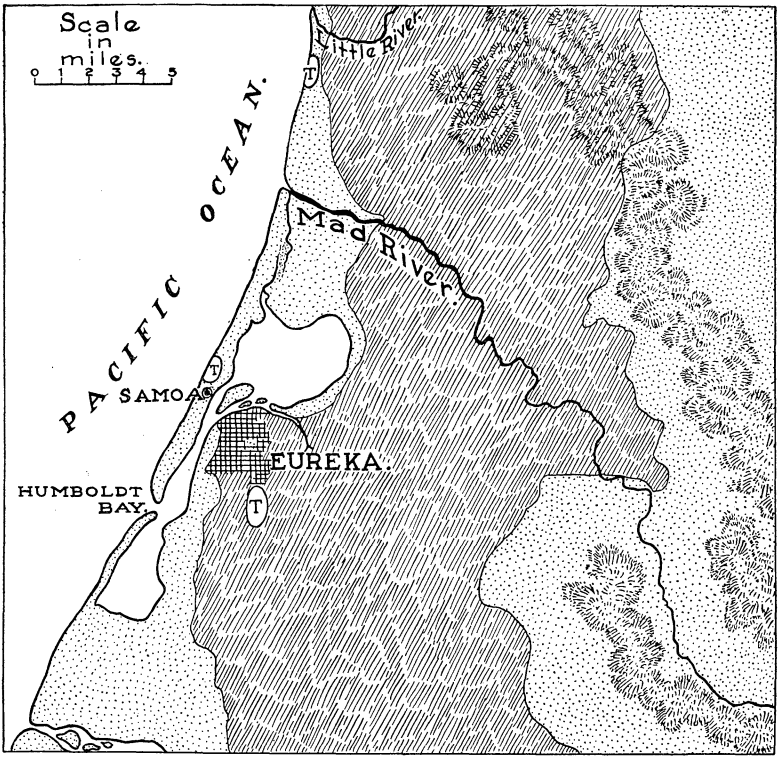

FIG. 1. Map of the vicinity of Humboldt Bay, California, based upon J. N. Lentell's map of Humboldt County. The three principal trapping stations are designated by the letter T. Area occupied by redwood forests is indicated by oblique shading.

more open areas a tall annual of the evening primrose family (*Epilobium angustifolium*) constitutes an important element in the vegetation.

One coming from the more arid parts of California can

not fail to be impressed by the prevailing humidity of both soil and atmosphere in this region. In the dense shade of the great redwoods the ground is damp, even during the summer months, and the fallen logs are covered with mosses and fungi.

When we cross Humboldt Bay to the narrow peninsulas separating this body of water from the ocean (Fig. 1), we enter a quite different environment. No redwoods are found, the woods, where present, are open, and the ground is prevailingly dry and sandy. In the wooded area, extending down the axis of the northern peninsula, the predominant tree is a small pine (*Pinus contorta*), though the waxberry and willow (*Salix hookeriana*) are likewise abundant, and small specimens of the Sitka spruce are fairly common. Among the more frequent shrubs are the huckleberry (*V. ovatum*), the twinberry (*Lonicera involucrata*) and silk tassel bush (*Garrya elliptica*). The ground is largely covered by two plants of trailing habit, the bearberry (*Arctostaphylos uva-ursi*) and the beach strawberry (*Fragaria chilensis*).

On its ocean side, the peninsula is bordered by a wide strip of shifting sand. Here the process of dune formation may be witnessed to perfection, the dunes often reaching a height of forty or fifty feet. In places the encroachments of the sand upon the hard-pressed vegetation are evidently rapid, solid ramparts of willows and spruces being steadily engulfed by an advancing wall, frequently as high as the trees themselves. Nevertheless, even on the open sands of the dunes, certain trailing plants maintain a precarious foothold. Among the commonest of these are to be mentioned the yellow sand verbena (*Abronia latifolia*), the beach strawberry (*F. chilensis*), beach pea (*Lathyrus littoralis*), and two species of Franseria (*F. chamissonis* and *F. bipinnatifida*), while the succulent *Mesembryanthemum aequilaterale* is occasionally met with.

Despite the nearness to the ocean and the high atmospheric humidity, the peninsula region seems dry in comparison with the redwood forests. This is due in part to

the loose, sandy character of the soil—where, indeed, any real soil exists—and to the comparative lack of shelter from the prevailing westerly winds. Evaporation here is doubtless more rapid than in the comparatively stagnant air of the forests.

To my surprise, the footprints of mice and other small mammals were abundant, even on the shifting sands, in the areas of sparsest vegetation. Since these tracks, for the most part, were effaced every day by the wind, the animals must have been present in large numbers. Indeed, it was in or close to the dune region that I trapped most of the twenty-eight *Peromyscus*. It seems more than possible, therefore, that the predominantly paler shade of the mice dwelling here may be due to the same causes which are operative in producing the yet paler hues of many of the desert rodents.

What the effective factors are can not yet be stated with certainty in either case. Protective coloration is of course an obvious explanation, but it is one of doubtful applicability in the case of animals which are almost wholly nocturnal in their habits. For this and other reasons it seems more likely that the pale coloration of these mice stands in some more direct relation to the humidity of their immediate surroundings. That it is not, however, a strictly "somatic" phenomenon, called forth anew in each generation, I have already shown for the desert race, *P. m. sonoriensis*.[9]

Whether or not the peculiar color of the pelage in the Samoa race is likewise hereditary I have endeavored to test experimentally. Seven living females and a number of males were brought to La Jolla in June, 1916. Unfortunately, it was not possible to obtain more than two broods of young, comprising three individuals, one male and two females. These animals were carefully examined at the age of five months, in comparison with over forty individuals, derived from the redwood stock, which were

[9] AMERICAN NATURALIST, Nov., 1915. I have since reared this race in Berkeley as far as the third (in one instance the fourth) cage-born generation, without any certain modification in color.

mainly of the same age or older, and likewise reared from birth at La Jolla. Not a single individual of the latter stock was as pale as either of the two females of Samoa parentage. The male of the Samoa race was, however, of about the average shade of the redwood descendants. As stated above, some of the wild parents, trapped on the peninsula, were likewise as dark as many of the redwood series.

No certain conclusions can, of course, be based upon these three individuals. But the condition of the two females certainly lends support to the belief that the peculiar coat color of the Samoa race, however it was acquired, has become fixed germinally.

Reference to the map shows that the northern peninsula of Humboldt Bay is largely isolated, so far as land-living rodents are concerned. In addition to the ocean and the bay, a marshy tract extends from the latter to the Mad River, which, in turn, interposes a further barrier on the north, and nearly converts the peninsula into an island. Beyond the mouth of Mad River, this same type of sand-dune formation extends uninterruptedly to the mouth of Little River, about six miles to the north, where it ends abruptly and the shore line becomes precipitous.

Now this northward extension of the sand-dune region is not isolated by any physical barrier from the redwood forest, which here comes near to the coast. It occurred to me, therefore, to attempt the collection of *Peromyscus* from a point somewhere within this region. The locality chosen was close to the ocean, about two miles south of Little River and four to five miles north of Mad River. Here the conditions were found to be closely similar to those on the exposed side of the northern peninsula of Humboldt Bay. The dunes were on the whole lower, however, and some minor differences were noted in the flora. The belt of shifting sand here ranges from five or six hundred feet to perhaps a fourth of a mile, giving place on the landward side to a narrow meadow or marshy area, succeeded by a high, steep, wooded ridge.

About ninety traps were set on two consecutive nights,

yielding in all forty-eight *Peromyscus,* all belonging to the subspecies *rubidus.* Many of these were still in juvenile pelage and such individuals were kept and allowed to mature in captivity.

A hasty comparison of the living Little River animals (as I shall call them) with those from the Samoa and Eureka trapping grounds made it plain that, in respect to color, they belonged with the latter group rather than the former. Careful comparisons of series of dead mice and of skins were made later and the bodies were subjected to the customary measurements. Owing to numerous deaths, however, only twenty-eight individuals were available for these purposes.

This more critical examination confirmed my earlier belief that the Little River mice agreed pretty closely, in average color, with the redwood stock, but that they differed widely from those taken on the peninsula. It seemed probable, however, that the mean shade was slightly lighter than that of the former animals, making them, to this extent, intermediate.

One conclusion then seemed plain. The peninsula race, exposed to certain modifying conditions, was enabled to differentiate from the mainland stock, owing to the almost insuperable barriers to migration. The Little River stock, exposed to practically the same conditions, have not formed a distinguishable race, because the rate of differentiation has been far exceeded by the rate of diffusion, or intermingling with the great body of more typical "*rubidus,*" dwelling in the redwood forests which extend back from the coast. We might seem to have, therefore, a particularly clear cut example of the effectiveness of isolation in the formation of a local race.

Now, I am not yet prepared to admit that such conclusions would be groundless. But here, as so often happens, a further study of the data has shown that the problem is more complex than was at first suspected. It is true that the mice of the more northern sand dunes have not formed a distinct race as regards *color.* But it is none the less certain that they differ from those of the

Eureka region in regard to both the length of the tail and that of the ear. In respect to the former character, they agree pretty closely with the Samoa race, the difference from the redwood stock being statistically even more certain in this case. To still further complicate the situation, we find that the ear, instead of being longer, is shorter than that of the redwood mice by about half a millimeter, and thus averages about one and one half millimeters shorter than in the peninsula race. Here, too, the differences are even more certain statistically than those which distinguish the Eureka and Samoa series.

The numbers are small, of course, only twenty-eight of the Little River mice having been available for measurement. But as regards tail length, the difference between the averages is seven to nine[10] times its probable error, so that the likelihood of its being due to random sampling is very small.

Have we, then, here merely another example of inconclusive data, which might best have been left unpublished? I do not think so. The mere existence of these local differences in color and in the size of parts deserves careful description, whatever interpretation we may place upon them.

Moreover, I am disposed to believe that the case of coat color is not entirely comparable with that of the length of the appendages. In another article[11] I have given reasons for thinking that some of the differences in the former may have arisen in nature as more or less direct effects of environmental conditions. On the other hand, I have shown that such an explanation would be of very difficult application as regards some of the measurable differences in the parts of the body, even though the latter are known to be readily influenced by various experimental agencies.

Now the evidence at hand is sufficient to show that any environmentally produced modifications of coat color are

[10] Depending on whether the comparison is made with the Eureka males or females, the sexes being combined in the case of the Little River group.

[11] AMERICAN NATURALIST, Nov., 1915.

at best rather gradual. *Rubidus* remains *rubidus* and *sonoriensis* remains *sonoriensis,* after several generations of captivity in changed climates. But even the first cage-born generation of each of my subspecies is found to be highly modified by confinement, in respect to the mean length of certain of the appendages. That this somatic plasticity would be accompanied by a high degree of germinal instability, as regards these parts, could not, of course, be predicted in advance. But the frequent appearance of local differences of type renders it probable that this is true. Whether or not these local peculiarities are due in some indirect way to environmental factors, or whether they are due to "spontaneous" mutation, need not concern us here. The main point to bear in mind is the probability that the pelage color is somewhat more stable in these mice than are the bodily proportions, despite the fact that it is the former, rather than the latter, which gives the clearest evidence of a definite correlation with known factors of the environment.

For the reason just stated, it is possible that the differentiation of a new color race might require fairly rigid isolation; whereas local differences in some of the measurable parts might arise in the presence of no other barrier than the naturally slow rate of diffusion of a non-migratory animal. As was remarked earlier, we have reason to suppose that representative collections from an indefinite number of localities would reveal the existence of statistically certain differences between the mice of many of these localities. In most cases, it would probably be unjustifiable to assign these series to distinct *races,* or other definite taxonomic groups, since it is likely that perfect intergradation would be found between most of them, and that the degree of difference would be largely a function of the distance apart of their respective habitats.

These last remarks are, of course, largely conjectural. Part of the author's present program consists in a careful study of local differences of the sort here discussed.

It is hoped that this will render possible more definite answers to some of these difficult questions.

It seems to be held by certain zoologists that any discernible difference between two local types, if at all constant, ought to be in some way recognized in the nomenclature. Indeed, I have been advised to name this modified race of *rubidus* from the northern peninsula of Humboldt Bay. Such a practise, if carried out consistently, would lead either to an endless multiplication of subspecies, or else to the introduction of quadrinomial names. Either procedure would, I think, be deplorable. The actual needs of the situation can commonly be met, I believe, by stating the locality from which a given specimen or collection was taken. The bestowing of formal names creates the false impression of a multitude of well-defined entities which do not, in reality, exist. Moreover, it is my firm conviction that nomenclature should have for its object the recognition of resemblances as well as the recognition of differences. The first of these functions is all too frequently overlooked.